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The potential for early generation selection to identify potato clones with resistance to Verticillium wilt

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Abstract Verticillium wilt (VW) of potato, caused primarily by the fungus *Verticillium dahliae,* results in yield loss and is therefore an important soil-borne disease. Resistance to VW exists in potato germplasm and is used by breeders during cultivar development. Breeders could make more rapid progress toward the development of VW resistant clones if they had an effective early generation selection strategy. The purpose of this study was to determine whether selection for VW resistance could be carried out in the first tuber generation on single hills. One hundred and fifty-two clones from 19 families were planted as single hills on a *V. dahliae*-infested field. Each plant was scored for vine maturity, VW symptom expression, yield, stem colonization (colony forming units (cfu), in dried basal stem segments) and incidence (percent infected stems). In the second clonal generation, which consisted of replicated four-hill plots, stem colonization scores and incidence values were used to identify clones which were more resistant than a moderately resistant cultivar and others which were more susceptible than a susceptible cultivar. The efficiency and reliability of the single-hill selection strategy, based on symptoms and yield, was then determined by comparison to the four-hill results. We determined that the best single-hill selection strategy was negative selection (discard clones with the lowest performance) with low stringency, based on yield.

Keywords Potato · *Solanum tuberosum* · Verticillium wilt · Early dying disease · *Verticillium dahliae*

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Introduction

Verticillium wilt (VW) is one of the most important yield-limiting diseases in potato production (Powelson and Rowe 1993). It is mainly caused by the soil borne fungi *Verticillium dahliae* Kleb, and *Verticillium albo-atrum* Reink and Berth. Soil fumigation is an effective control strategy, but it is often cost prohibitive and the use of fumigants results in negative environmental and human health effects (Rowe et al. 1987). Fumigants also destroy beneficial microflora and fauna in the soil (Pegg 1974). Host resistance is thought to be the most promising method of managing VW. A few commercial cultivars such as 'Ranger Russet,' 'Ranger Nugget,' 'Reddale' and 'Defender' are reported to have moderate levels of resistance to VW but these cultivars have not replaced the most widely grown varieties (Frost et al. 2006; Rowe and Powelson 2002). Therefore,

efforts have been employed to find highly resistant sources from diploid wild species and also to improve the efficiency of breeding methods for VW resistance in potato (Concibido et al. 1994; Jansky and Rouse 2000, 2003; Jansky et al. 2004).

In a typical potato breeding program, tens of thousands of seedling tubers are screened for superior genotypes every year. Over 95% of the seedlings are usually discarded in the first tuber generation, based on visual evaluations of tuber appearance in the field. Selection for resistance and quality traits is typically delayed until later generations, when the number of clones has been reduced (Louwes and Neele 1987). Breeders, however, are interested in determining whether they can effectively select for resistance and quality traits in early generations. The efficiency of early generation selection results from identifying and retaining superior genotypes before the population size has been dramatically reduced (Caligari et al. 1986). Stringent early generation selection is usually ineffective with complex agronomic tuber characteristics because of their low heritabilities and because visual evaluation is inaccurate (Anderson and Howard 1981; Brown et al. 1987; Love et al. 1997). As a compromise, Tai and Young (1984) suggested using a moderate intensity of selection in the seedling generation. In addition, they suggested that discarding the clones with the worst performance (negative selection) is most effective for traits based on visual discrimination. Several studies have pointed out that early generation selection decisions should be based on individual component traits. For example, if a trait exhibits a low heritability estimate and inconsistency of expression, it would not be successful for early generation selection (Gopal et al. 1992; Love et al. 1997; Maris 1988).

Successful early generation seedling selection for disease resistance requires rapid disease development in the most susceptible seedlings, so selection can be carried out based on distinct differences between susceptible and resistant plants. An effective system to simultaneously screen for resistance to potato virus Y (PVY), potato cyst nematode (*Globodera rostochiensis* and *G. pallida*) and late blight (*Phythophthora infestans*) in the first and second clonal years has been reported (Jellis et al. 1986). In Poland, seedling selection has been effective in developing clones resistant to potato viruses X, Y, A, and S because simple screening methods exist and symptom expression is clear in potato. However, selection for potato leaf roll virus resistance is difficult because no extreme resistance exists and no convenient methods of selection are available (Swiezynski 1984). Stewart et al. (1994) reported that selection of seedling plants with resistance to early blight is a useful strategy for the development of resistant clones.

Several methods have been employed to determine VW disease severity in potato, including visual assessment for symptom expression in infested fields (Jansky and Rouse 2000), yield loss between infested and non-infested fields (Frost et al. 2007; Susnoschi et al. 1976), and quantification of fungal colony forming units (cfu) in fresh sap or air dried stems (Corsini et al. 1990; Davis et al. 1983; Hoyos et al. 1991). There are few reports on the potential for early generation selection to identify VW resistance in potato breeding programs. Hoyos et al. (1993) assayed vascular colonization by *V. dahliae* in seedling transplants and identified resistant clones. Only 8.6% of the putatively resistant clones selected as seedlings were resistant in the first clonal generation. However, the authors suggested that selection pressure may have been too low in that study. Corsini and Pavek (1996) observed that early generation screening strictly for VW resistance was associated with extreme lateness, including lack of tuber size and poor storability. Consequently, clones with high yield tended to be eliminated. Therefore, they suggested that early generation screening for VW resistance should be accompanied by selection for high yield.

The goal of this study was to determine whether clones in the first tuber generation could be selected for VW resistance based on assessments that could be easily carried out by breeders on a large scale. The experiment was designed to determine whether symptom expression, yield or the combination of the two traits evaluated on a *V. dahliae*-infested field could be used to effectively identify VW resistant genotypes grown in single hill plots. In order to determine whether selection was effective, clones were phenotyped for resistance based on replicated multiple hill trials in the second year of the study.

Materials and methods

Plant material

A total of 152 clones from 19 families (38 diploid and 114 tetraploid) was planted at the Hancock, Wisconsin, Agricultural Experiment Station. Clones were planted

in a randomized complete block design grown using standard cultural practices and recommended best management practices for pest and disease control. In the single hill experiment (first clonal generation), two single-hill replications were planted with 60 cm within-row spacing on a *V. dahliae*-infested field on May 12, 2004. In the four hill experiment (second clonal generation), three four-hill replications were planted with 30 cm within-row spacing on the same field used in the single hill experiment on 9 May, 2005. In addition, 20 parent clones, a susceptible control ('Russet Burbank') and a moderately resistant control ('Ranger Russet') were included in the four hill experiment.

Disease assessment

Each plant was scored for vine maturity and VW symptom expression two times during the potato growing season (3 August/23 August in the single-hill trial and 24 July/17 August in the four-hill trial). Maturity was scored on a 1 (senescent) to 5 (pre-flowering) scale. Symptoms were assessed by estimating the percent of a plant's leaf area exhibiting necrosis, chlorosis, and/or wilting. Although symptom expression data were collected on only two dates in each year, these dates were chosen based on maximum disease expression. A previous study with potato late blight found that two strategically scheduled observations can quantify disease as reliably as a large number of observations (Haynes and Weingartner 2004). For yield evaluation, tubers were harvested from each plot and total tuber weight was measured. Just prior to harvest, basal stem segments of primary stems were collected from each plant. Stems were dried at room temperature for one month and ground in a Wiley mill with a 40-mesh screen. After each sample was ground, the mill was thoroughly cleaned with a vacuum cleaner to remove all debris. A 50 mg sample from each stem was plated on a petri dish (10 cm) containing nutrient pectate agar (NPX) medium as a selective medium (Butterfield and DeVay 1977). Following a two-week incubation period at room temperature in the dark, the number of *V. dahliae* colonies in each petri dish was counted as a measure of stem colonization.

Soil assessment

Just prior to harvest, soil samples were collected from 24 to 30 randomly chosen plots in both years. Soil samples were dried for 1 month at room temperature. Three 10 g subsamples from each soil sample were placed into a 250 ml flask to which 100 ml deionized water was added and stirred for at least 10 s. Two 1 ml aliquots from each flask were plated on NPX medium and spread evenly with a glass rod. After a two-week incubation period in the dark, the number of *V. dahliae* colonies was counted on each plate using a dissecting microscope.

Field inoculation

To ensure uniform infection in the field, the four-hill experiment plot was inoculated by spreading dried, ground *V. dahliae*-infested rye seeds in an open furrow at planting (Platt and Sanderson 1987). The furrow was closed after planting. To create the rye inoculum, seeds were soaked in distilled water overnight, drained, placed into plastic bags and autoclaved twice at 121°C for 70 min each time. The V18 isolate of *V. dahliae* race 4A from severely infested potato fields was cultured in Czapek media for one week. A 10 ml aliquot of the V18 conidial suspension (6×10^6 cfu/mL) was injected into each bag containing 1 kg of rye seeds. Inoculated rye seeds were incubated for 2 months at room temperature. The inoculum was then air-dried and ground in a Wiley mill with a 60-mesh screen. A 2 g aliquot of ground rye inoculum containing 10^4 cfu/g was spread on the soil around each seed tuber.

Analysis of data

In order to determine whether single hill selection was effective, we characterized resistance in all clones based on the replicated trial carried out on the four hill experiment in the second clonal generation. Resistance was determined based on colonization incidence (number of infected stems) and propagule population size (number of cfu in each stem) in stems collected from the four hill experiment. Colony counts were transformed using $(\log n + 1)$ prior to analysis of variance and each six-stem sample was averaged after transformation. Symptom progression in each of the two seasons was summed to calculate the area under the disease progress curve (AUDPC). The AUDPC's across the 2 years were normalized to create relative AUDPC (RAUDPC) scores, allowing comparisons across years. An analysis of variance

was performed on each data set using the General Linear Model in SAS v.9.0 (SAS Institute, Raleigh, NC). Spearman rank correlation coefficients were calculated using SAS.

Results

Soil samples indicated that, in both years, clones were subjected to severe pathogen pressure (approximately 50 cfu/g). Resistant clones were identified based on stem colonization by *V. dahliae* in plants from the four hill experiment in 2005. Since six stems were collected from each of three replications, a total of 18 main stems was scored for most clones. Propagule population size within stems and incidence of infected stems were closely correlated with each other ($r = 0.95$, $P < 0.001$). Clones were considered to be resistant if both values were numerically less than those of the moderately resistant control 'Ranger Russet' ($\log_{10}$ (cfu/g + 1) = 1.56, 72% incidence). Clones were considered susceptible if one of the stem colonization values and incidence were more than 'Russet Burbank' as the reference susceptible control ($\log_{10}$ (cfu/g + 1) = 2.34, 83% incidence). As a result, 52 clones more resistant than Ranger Russet and 45 clones more susceptible than Russet Burbank were identified (Fig. 1). Maturity, yield, and disease data for the parents and controls are listed in Table 1. Some parents were more resistant than Ranger Russet, while others were more susceptible than Russet Burbank.

In order to evaluate the consistency of scores across years, Spearman rank correlation tests were carried out. Incidence was not included in this analysis, since single hill data often did not include multiple stems. Table 2 shows highly significant correlations ($P < 0.001$) between the single- and four-hill experiments for maturity, RAUDPC, yield, and stem colonization. It is interesting that rankings across years were most consistent for yield and least consistent for stem colonization.

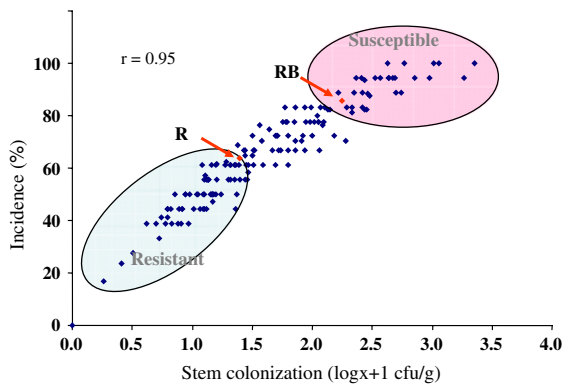

Fig. 1 Separation of clones into groups that are more resistant than the resistant control Ranger Russet (R) and more susceptible than the susceptible control Russet Burbank (RB)

Table 2 also shows rank correlations among variables in each of the 2 years of the study. In both years, maturity was negatively correlated with disease symptoms. That is, early maturing clones tended to have higher symptom expression. In addition, in both years, stem colonization severity was highly correlated with incidence of stem colonization. There were no other consistent trends across years.

In order to determine the effectiveness of selection in the single-hill experiment based on symptoms and/or yield, clones identified as more resistant than Ranger Russet or more susceptible than Russet Burbank were plotted with yield against symptom expression (Fig. 2). As Fig. 2 indicates, resistant and susceptible clones overlap. However, there were some resistant clones with higher symptom expression than susceptible clones. Symptom expression was likely affected not only by disease but also maturity. To explore this idea, maturity was plotted against symptom expression using single hill data (Fig. 3). Most of the susceptible clones with high stem colonization showed late maturity.

Symptom expression and apparent yield can be easily applied for single hill selection, since breeders typically reduce population size during early generations by visual assessment with various levels of selection stringency. Table 3 illustrates the results from three selection stringencies. The percentage of resistant clones identified in the single hill trial decreased as the stringency of selection increased. At the 40% selection level, the best predictor of resistance was the combination of yield and symptoms; 38% of the clones selected for resistance in the single hill trial were classified as resistant based on stem colonization in the four-hill trial.

Discussion

This study was carried out to determine whether selection in the first tuber generation for low symp-

Table 1 Field performance of clones used as parents and standards in the four hill trial

Clone	Maturity	RAUDPC	Yield (g)	Stem colonization (cfu/50 mg)	Incidence (% stems infected)
Andover	2.00	0.55	1110.30	59.58	61
C159	1.67	0.33	397.00	15.55	56
C181	1.50	0.28	460.50	103.25	100
C182	1.50	0.38	531.50	88.00	75
C33	2.50	0.24	737.00	60.70	58
C341	1.00	0.27	1077.00	61.34	92
C385	1.50	0.38	567.00	136.84	100
C392	1.00	0.21	340.00	152.00	50
C396	1.67	0.48	231.30	36.78	67
E-29-1	2.33	0.44	146.30	5.87	60
E-51-2	2.67	0.21	619.00	57.55	89
E-51-4	4.00	0.13	1027.50	130.84	100
MN85432	1.50	0.45	652.00	176.25	100
ND3828-15	2.33	0.32	1326.30	129.61	83
S438	1.00	0.28	1152.70	20.08	72
S440	1.00	0.60	1327.30	5.00	50
Snowden	2.33	0.21	1445.70	32.17	83
W1355-1	1.67	0.34	1668.00	37.28	78
Yukon Gold	1.00	0.66	1625.70	12.44	72
Zarevo	1.67	0.18	1072.70	42.28	67
Ranger Russet	2.00	0.18	1216.70	14.50	72
Russet Burbank	2.33	0.31	1238.30	65.94	83

Table 2 Spearman rank correlation coefficients (r) among maturity, RAUDPC, yield, stem colonization, and incidence scores within year and between years

Between years		Maturity	RAUDPC	Yield	LM[a]	IC (%)
2005/2004:	Coefficient (R)	0.51***	0.59***	0.69***	0.33***	–
Within year						
2005	Maturity	–	−0.55***	−0.33***	0.31***	0.26***
	RAUDPC	–	–	0.08	−0.41***	−0.38***
	Yield	–	–	–	0.10*	0.10*
	LM	–	–	–	–	0.95***
2004	Maturity	–	−0.57***	0.04	−0.03	0.01
	RAUDPC	–	–	−0.05	0.04	−0.03
	Yield	–	–	–	0.04	−0.02
	LM	–	–	–	–	0.73***

* $P < 0.05$, *** $P < 0.001$

[a] Log transformed stem colonization (log cfu/g + 1)

tom expression and/or high yield in a *V. dahliae*-infested field can identify clones with resistance to VW. These traits would be easy for a breeder to score, allowing selection to occur simultaneously for tuber type and VW resistance. With a low selection stringency (80% of single hills retained), about ¾ of the

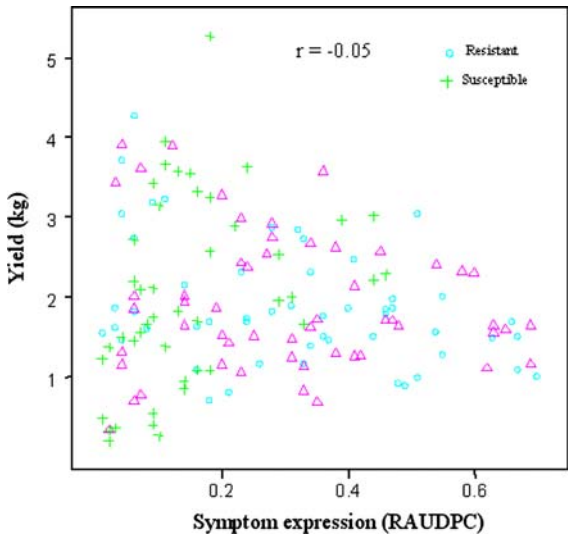

Fig. 2 Yield and symptom expression of clones that are more resistant than the resistant control Ranger Russet (o) and clones that are more susceptible than the susceptible control Russet Burbank (+). All other clones are indicated by a triangle

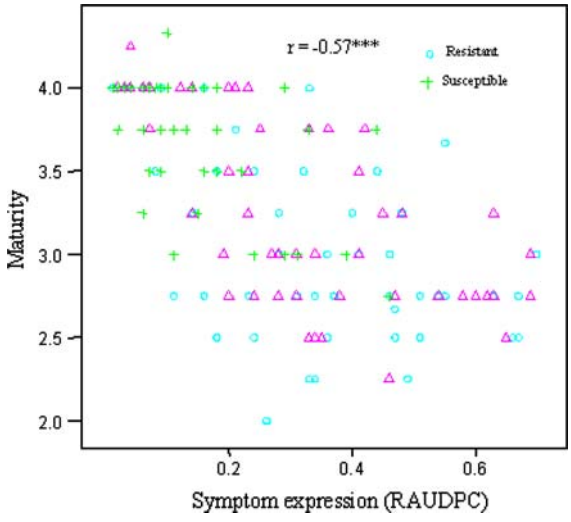

Fig. 3 Maturity and symptom expression of clones that are more resistant than the resistant control Ranger Russet (o) and clones that are more susceptible than the susceptible control Russet Burbank (+). All other clones are indicated by a triangle

clones selected as single hills are resistant (Table 3). At the other end of the spectrum, a high selection stringency (40% of clones retained) results in a population in which only 1/3 of the clones are resistant. However, if 40% of the seedlings are discarded based on yield, then nearly 60% of the remaining clones will be resistant. This may be the most desirable compromise between selection stringency and effective identification of resistant clones. Selection for high yield may also help to avoid selecting for late maturity and immature plant resistance. Corsini and Pavek (1996) also suggested that selection for VW resistance should be based on yield and other agronomic criteria in *V. dahliae*-infested fields, since selecting at early stages of variety development strictly for VW resistance based on foliar wilt symptoms and stem colonization was inefficient. However Susnoschi et al. (1976) found it difficult to find a direct association between yield and VW resistance in the field because other diseases and abiotic stresses also affect yield.

Table 3 Effect of selection stringency and single hill selection criterion on the percent of selected clones in both years

Selection criterion	80[a]	60	40
Symptoms	75[b]	49	30
Yield	79	59	36
Yield + Symptoms[c]	77	53	38

[a] Percent clones retained in single hill trial (selection stringency)

[b] Percent of common clones selected in single-hill that were selected in four-hill trial based on stem colonization

[c] Both yield and symptom expression

Strong correlations between the single- and four-hill trials indicate a degree of consistency in ranks across years. Surprisingly, the strongest correlation was between yield of single hill plots and that of four-hill plots. We expected that differences in seed size and quality in single hills generated from seedlings would lead to large variations in yield that would not be as apparent in multi-hill plots generated from tubers. Stem colonization scores showed the weakest relationship across years. Although stem colonization is commonly used to determine VW resistance, scores can be variable across years. Frost et al. (2007) also found that absolute scores and rankings based on stem colonization can vary across years. Inoculum distribution may not be evenly distributed in the soil, resulting in variability among individual roots for exposure to *V. dahliae*. In addition to inherent variability in plant infection and pathogen development across years, differences among the two trials may have also been important. The single-hill trial relied on natural inoculum in the field, while each plot in the four-hill trial was inoculated, reducing the possibility of escapes. Also, many clones had only one stem in the

single hill trial, while six stems were collected from each plot in the four-hill trial. Stem-to-stem variability for stem colonization scores can be high, even among stems of the same plant (Frost 2005). Consequently, colonization data from a single stem may not accurately predict resistance. It is common to evaluate plants in infested fields as a measure of VW resistance (Jansky and Rouse 2000; Rowe et al. 1987). However, as seen in this and other studies, variability in pathogen populations and host-plant-environment interactions can influence resistance ratings (Frost et al. 2007; Wheeler et al. 2000).

The correlation between symptom expression (RAUDPC) or yield in single hills in 2004 and stem colonization (LM) in 2005 provides an indication of whether single hills can be visually selected for VW resistance. It is not feasible to select single hills in a breeding program based on stem colonization. Therefore, breeders are left with symptom expression or yield as selection criteria in the single hill stage. Although statistically significant, correlation coefficients were numerically low between symptom expression in 2004 and stem colonization in 2005 ($r = -0.31$, $P < 0.0001$) and between yield in 2004 and stem colonization in 2005 ($r = 0.09$, $P < 0.27$. Because these values are low, breeders can not effectively select for resistance in single hills and should wait until later stages to identify VW resistant clones.

Rank correlations between variables within single- and four-hill experiments indicated that relationships between variables were stronger in the four-hill experiment (Table 2). Three replications of a four-hill trial should reduce the effects of outliers, escapes, tuber size variation, and plant vigor. In both years, late maturity was strongly correlated with low symptom expression. However, severe symptom expression was associated with low stem colonization in the four-hill trial. Symptom expression may have been mistaken for natural senescence, since they are similar in appearance. On the contrary, late maturing clones did not show foliar symptom expression even though *V. dahliae* was detected in stems. These clones often expressed immature plant resistance, which is usually accompanied by low yield.

In order to test the effectiveness of single hill selection, clones were characterized for resistance based on stem colonization in the replicated four-hill trial where a large number of stems were available (Fig. 1). Stem colonization is generally considered to be the "gold standard" for resistance evaluation, since it measures the pathogen population in the plant. While we used this method to determine the relationship between "true" resistance (in the four-hill trial) and "putative" resistance based on yield and symptom expression (in the single hill trial), it is not a practical method for identifying resistance in single hills. First of all, it would be too time-consuming for breeders to plate stem samples from thousands of single hills. In addition, data from a single hill are based on only a few stems and may not provide a representative sample for resistance screening.

Interestingly, most susceptible clones based on stem colonization in this study were late maturing, with low symptom expression (Fig. 3). Treadwell (1991) also made this observation. In contrast, Corsini and Pavek (1996) observed a correlation between late maturity and low stem colonization. The direction of the correlation between maturity and stem colonization may depend on the genetic composition of the population. To address this complication, clones could be grouped based on maturity and then assessed for symptoms within maturity groups (Treadwell 1991). This would be difficult to implement at the single hill stage, though, unless perhaps families could be grouped based on parental maturity scores.

As discussed above, stem colonization is typically considered to be a better method of resistance evaluation than symptom expression because it measures actual pathogen levels in plant tissues. The correlation between stem colonization and symptom expression was low in both years (Table 2). These data highlight the difficulty in using symptom expression to identify clones with true VW resistance. Clones with low symptom expression may be tolerant instead of truly resistant. These clones are undesirable because they add inoculum to successive potato crops even when rotation practices are used. In contrast, a high correlation was observed between stem colonization (levels of the pathogen in stems) and incidence (the number of infected stems). The correlation was very high in 2005, when the data were most accurate because plot sizes were larger, more replications were evaluated and plots were inoculated, reducing the possibility of escapes. These results are similar to those in previous correlation studies (Jansky and Rouse 2000). Consequently, instead of counting cfu in stems, resistance could be determined by counting the number of stems that contain any fungal propagules.

Breeders practice visual selection at the single hill stage. While traits such as tuber appearance, set, and size are important, overall yield is considered as well. Because selection pressure is so severe in single hill populations, low-yielding clones are not selected. The rank correlation between yield in single hills and yield in four hill plots was relatively high (0.69) and statistically significant (Table 1). Consequently, when breeders select single hill clones based on yield, they are most likely selecting clones with good yield potential.

Overall, this study indicates that single-hill selection for VW resistance would be most effective when clones are discarded based on yield using a moderate level of stringency. Pathogen quantification methods would be best applied as early as possible, but when multiple stems are available. The potential problem of seed transmission of the pathogen would also be avoided by delaying field evaluations for VW resistance until genotypes are replicated (Omer et al. 2000). Duplicates of the test clones could be planted on a clean field for maintenance. Since stem plating is low through-put and time demanding, a simple and reliable quantification method would enhance the likelihood of identifying highly resistant clones. Recently, quantitative PCR has been developed and is efficient and specific to *V. dahliae* (Atallah et al. 2007; Bae et al. 2007). There has been an effort to develop molecular markers to apply marker assisted selection for VW resistance in potato (Simko et al. 2003, 2004; Bae et al. 2008). Therefore in near future, these methods should be considered for the identification of VW resistant clones in early generations. A good strategy for single-hill selection may be to discard 50–60% of the worst yielding clones and then apply Q-PCR or marker assisted selection to reduce an additional 30–40% of clones. Only 10% of clones will be saved for more thorough selection in later generations. Family selection at the single hill stage might also improve selection efficiency. For example, four of the 10 most VW resistant clones came from a single 4x × 2x cross between two of the most resistant parents (S438 × C396). Perhaps selection intensity could vary depending on the resistance levels of the parents.

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References

Anderson JAD, Howard HD (1981) Effectiveness of selection in the early stages of breeding programmes. Potato Res 24:289–299

Atallah ZK, Bae J, Jansky SH, Rouse DI, Stevenson WR (2007) Multiplex real-time quantitative PCR to detect and quantify *Verticillium dahliae* colonization in potato lines that differ in response to Verticillium wilt. Phytopathology 97:865–872

Bae J, Atallah ZK, Jansky SH, Rouse DI, Stevenson WR (2007) Colonization dynamics and spatial progression of *Verticillium dahliae* in individual stems of two potato cultivars with differing responses to potato early dying. Plant Dis 91:1137–1141

Bae J, Halterman D, Jansky SH (2008) Identification of a molecular marker associated with Verticillium wilt resistance in diploid interspecific potato hybrids. Mol Breed. doi:10.1007/s11032-008-9156-8

Brown JC, Caligari PDS, Mackay GR, Swan GEL (1987) The efficiency of visual selection in early generation of a potato breeding programme. Ann Appl Biol 110:357–363

Butterfield EJ, DeVay JE (1977) Reassessment of soil assays for *Verticillium Dahliae*. Phytopathology 67:1073–1078

Caligari PDS, Brown JC, Abbott BJ (1986) Selection for yield and yield components in the early generation of a potato breeding programme. Theor Appl Genet 73:218–222

Concibido VC, Secor GA, Jansky SH (1994) Evaluation of resistance to Verticillium wilt in diploid, wild potato interspecific hybrids. Euphytica 76:145–152

Corsini DL, Pavek JJ (1996) Agronomic performance of potato germplasm selected for high resistance to Verticillium wilt. Am Potato J 73:249–260

Corsini DL, Pavek JJ, Davis JR (1990) Verticillium wilt resistant potato germplasm: A66107–51 and A68113–4. Am Potato J 67:517–525

Davis JR, Pavek JJ, Corsini DL (1983) A sensitive method for quantifying *Verticillium dahliae* colonization in plant tissue and evaluating resistance among potato genotypes. Phytopathology 73:1009–1014

Frost KE (2005) Potato breeding for Verticillium wilt resistance in potato (*Solanum tuberosum*). M.S. Thesis, University of Wisconsin, 205 pp

Frost KE, Jansky SH, Rouse DI (2006) Transmission of Verticillium wilt resistance to tetraploid potato via unilateral sexual polyploidization. Euphytica 149:281–287

Frost KE, Jansky SH, Rouse DI (2007) Consideration for Verticillium wilt resistance evaluation in potato. Plant Dis 91:360–367

Gopal J, Gaur PC, Rana MS (1992) Early generation selection for agronomic characters in a potato breeding programme. Theor Appl Genet 84:709–713

Haynes KG, Weingartner DP (2004) Use of area under the disease progress curve to assess resistance to late blight in potato germplasm. Am J Potato Res 81:137–141

Hoyos GP, Zambino PJ, Anderson NA (1991) An assay to quantify vascular colonization of potato by *Verticillium dahliae*. Am Potato J 68:727–742

Hoyos GP, Lauer FI, Anderson NA (1993) Early detection of Verticillium wilt resistance in a potato breeding program. Am Potato J 70:535–541

Jansky SH, Rouse DI (2000) Identification of potato interspecific hybrids resistant to Verticillium wilt and determination of criteria for resistance assessment. Potato Res 43:239–251

Jansky SH, Rouse DI (2003) Multiple disease resistance in interspecific hybrids of potato. Plant Dis 87:266–272

Jansky SH, Rouse DI, Kauth PJ (2004) Inheritance of resistance to *Verticillium dahliae* in diploid interspecific potato hybrids. Plant Dis 88:1075–1078

Jellis GH, Lacey ND, Boulton RE, Currell SB, Squire AM, Starling NC (1986) Early generation screening of potato clones for disease and pest resistance. Asp Appl Biol 13:301–305

Louwes KM, Neele AEF (1987) Selection for chip quality and specific gravity of potato clones: possibilities for early generation selection. Potato Res 30:241–251

Love SL, Werner BK, Pavek JJ (1997) Selection for individual traits in the early generations of potato breeding program dedicated to producing cultivars with tubers having long shape and russet skin. Am Potato J 74:199–213

Maris B (1988) Correlations within and between characters between and within generations as a measure for the early generation selection in potato breeding. Euphytica 37:205–224

Omer MA, Johnson DA, Rowe RC (2000) Recovery of *Verticillium dahliae* from North American certified seed potatoes and characterization of strains by vegetative compatibility and aggressiveness. Am Potato J 77:325–331

Pegg GF (1974) Verticillium diseases. Rev Plant Pathol 53:157–182

Platt HW, Sanderson JB (1987) Comparison of inoculation methods for field studies on varietal response to Verticillium wilt of potatoes. Am Potato J 64:87–92

Powelson ML, Rowe RC (1993) Biology and management of early dying of potatoes. Annu Rev Phytopathol 31:111–126

Rowe RC, Powelson ML (2002) Potato early dying: management challenges in a changing production environment. Plant Dis 86:1184–1193

Rowe RC, Davis JR, Powelson ML, Rouse DI (1987) Potato early dying: causal agents and management strategies. Plant Dis 71:482–489

Simko I, Costanzo S, Haynes KG, Christ BJ, Jones RW (2003) Identification of molecular markers linked to the Verticillium wilt resistance gene homologue in potato (*Solanum tuberosum* L.). Acta Hortic 619:127–133

Simko I, Haynes KG, Ewing EE, Costanzo S, Christ BJ, Jones RW (2004) Mapping genes for resistance to *Verticillium albo-atrum* in tetraploid and diploid potato populations using haplotype association tests and genetic linkage analysis. Mol Genet Genom 271:522–531

Stewart H, Bradshaw JE, Wastie RL, Mackay GR, Orlyerlich L, Livescu L, Nachmias A (1994) Assessing progenies of potato for resistance to early blight. Potato Res 37:257–269

Susnoschi M, Krikun J, Zuta Z (1976) Trial of common potato varieties in relation to their susceptibility to Verticillium wilt. Potato Res 19:323–334

Swiezynski KM (1984) Early generation selection methods used in polish potato breeding. Am Potato J 6:385–394

Tai GCC, Young DA (1984) Early generation selection for important agronomic characteristics in a potato breeding population. Am Pot J 6:419–434

Treadwell FJ (1991) Breeding for resistance to Verticillium wilt in potato. PhD Dissertation, University of Minnesota

Wheeler TA, Madden LV, Rowe PR (2000) Effects of quadrat size and time of year for sampling of *Verticillium dahliae* and lesion nematodes in potato fields. Plant Dis 84:961–966